

<http://www.pjbs.org>

PJBS

ISSN 1028-8880

Pakistan Journal of Biological Sciences

ANSI*net*

Asian Network for Scientific Information
308 Lasani Town, Sargodha Road, Faisalabad - Pakistan

Combining Ability and Standard Heterosis Analysis of Two-Line System Hybrid Rice

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Abstract: Five indica photo-thermo sensitive genic male sterile (PTGMS) lines as female parents and 5 restorers lines as male parents were used to make 25 F_1 hybrids by diallel cross to study the combining ability and standard heterosis of 10 agronomic traits. The results showed that the characters of PTGMS lines are determined by the effects of general combining ability (GCA) and specific combining ability (SCA) of both the sterile and restorer lines and the GCA was found to be more effective. Pei'ai64S was the best general combiner among sterile lines followed by NS30g, while the Minghui63 was the best general combiner among the restorer lines followed by Sh623. Significant differences in combining ability among the sterile lines and positive correlation between the values of GCA and standard heterosis of hybrids were observed. The higher GCA of parents exhibited stronger standard heterosis in hybrids.

Key words: Combining ability, standard heterosis, two-line hybrid rice

Introduction

Rice is the main staple for a large segment of the world population. Heterosis, or hybrid vigor is a term used to describe the phenomenon in which the performance of an F_1 , generated by crossing of two genetically different individuals, is superior to that of the better parent (Xiao *et al.*, 1996). Heterosis is the foundation of the great success of hybrid rice in China. From 1976, during which hybrid seeds were first released to rice farmers, to 1991 during which the planted acreage of hybrid rice accounted for 55% of total planted area of paddy rice in China, the cumulative increased grain yield from planting hybrid rice amounted to more than 200 million tons. It has been demonstrated empirically that hybrid rice varieties have 15-20% yield advantage over the best conventional inbred varieties using similar cultivation conditions (Yuan, 1992).

Many Chinese rice scientists have been exploring new technological approaches to replace the cytoplasmic male sterile (CMS) system. So far, the most successful outcome is the development of two-line hybrids. This method is based on two new kinds of rice genetic tools: photoperiod-sensitive genic male sterile (PGMS) lines and thermo-sensitive genic male sterile (TGMS) lines that have been successfully developed in China recently and also has already entered into production and applied stage (Xiao *et al.*, 1995; Yuan, 1994). Two-line hybrid rice has a strong standard heterosis because, their male sterility is mainly controlled by one or two pairs of recessive nuclear genes, it has no relation to cytoplasm and it is free from the constraining of the definite restoration-maintenance relationship, so making full use of parent with good economical characters and general combining ability (GCA) increases the breeding opportunity of strong heterosis combinations (Yuan, 1994).

Combining ability is a measure of gene action (additive and non-additive). The GCA effects largely involve additive gene effects, whereas specific combining ability (SCA) effects represent only non-additive gene action. The presence of non-additive genetic variance offers scope for exploration of heterosis (Yadav *et al.*, 1999). The parents with good GCA can be used to obtain hybrids with strong heterosis and SCA

(Yan *et al.*, 2000). The experience of sterile line breeding showed that indica hybrid, japonica hybrid or crossing of indica and japonica had close correlation between economic traits and grain weight heterosis and combining ability of parents, especially the combining ability of sterile line was more important (Lu, 2000). The rice researchers around the world carried out studies on the combining ability of different kinds of rice (Sun *et al.*, 1993; Li *et al.*, 1990; Gong *et al.*, 1993; Chen *et al.*, 1997) and their achievements in this aspect can guide the use of heterosis in rice and the selecting of parents in hybridization of breeding.

To develop hybrid rice with higher yield, better grain quality and multiresistance is very important and the key is to breed PTGMS lines with good combining ability.

The present investigation was aimed to estimate the combining ability and standard heterosis of agronomic traits in five photo-thermo sensitive genic male sterile lines with five restorer lines.

Materials and Methods

Twenty five hybrid combinations were produced from 5 photothermo sensitive genic male sterile (PTGMS) indica lines including Pei'ai 64S (as a control of sterile line), new breeding PTGMS lines NS30a, NS30f, NS30h and NS30g all coming from combination descent of XinguangS//XinguangS/TG8, which the donor of sterile gene was Xinguang S were used as females, crossed with 5 diverse restorer lines namely Minghui 63, Rp5, Tt72, Sh633 and Sh623 were used as males by diallel way. All the hybrids, their parents and Shanyou 10 as a check variety (for working out standard heterosis) were sown on May 10th 2000 and transplanted on June 4th in experimental field area of Zhejiang University, Hangzhou, China. The plots were designed by randomized complete block design (RCBD) with three replications. Each plot had three rows with 5 single plants in each row, transplanting distance was a 20 cm inter and 15 cm intra-row spacing.

The observations were recorded on five plants per plot selected at random from each treatment in each replication. Ten agronomic traits were measured including days from sowing to initial heading (DHI), plant height (PH) (cm), number

of panicles per plant (NPP), panicle length (PL) (cm), number of spikelets per panicle (NSP), filled spikelets per panicle (FSP), seeds set rate (SSR) (%), grain weight per plant ($_{GWP}$) (g), flag leaf length of main culm (FL) (cm), 100-grain weight (100-GW) (g).

The combining ability analysis was carried out by Mo (1982) model and standard heterosis of hybrids for the characters were calculated over the check variety using Microsoft Excel.

Results

Analysis of variance: Analysis of variance for combining ability (Table 1) revealed highly significant differences of GCA and SCA variances for all the characters, which indicated that, both of additive and non-additive gene actions were involved in the control of the expression of these characters. The relative magnitude of estimates of GCA variance was higher than those of SCA variance for all the characters, indicating the importance of additive gene action.

Estimation of general combining ability (GCA): Among the 10 agronomic traits of PTGMS lines, the GCA of DH, NPP and GWP in NS30g line was higher than other female lines (Table 2). The Pei'ai 64S had the highest GCA of PH, PL, NSP, FSP and FL. While NS30h line had the highest GCA for SSR and 100-GW characters. Among the 10 agronomic traits of the restorer lines, the GCA of DH, PH, NSP and FL in Sh623 line was the highest compared with other male lines (Table 2). The Minghui 63 line had the best GCA of PL, FSP, SSR, GWP and 100-GW. While the GCA of Tt72 line was better than other restorer lines in NPP.

Evaluation of the parents: The results of combining method proposed by Wang (1981) are shown in Table 3. The data in the table are from the ranking numbers of GCA and according to the total marks, the evaluation of the parents was made. As the results showed in Table 3, among the female lines Pei'ai64S was the best general combiner followed by NS30g

Table 1: Analysis of variance for randomized complete block data for 10 agronomic traits

Source of variation	DF	DH	PH (cm)	NPP	PL (cm)	NSP
Mean	1	517340.34**	764845.0**	27545.50**	45612.05**	1966962.00**
GCA	8	99.63**	463.74**	53.02 ⁰ *	13.12**	3706.61**
SCA	16	13.30**	46.50**	32.85**	4.12**	799.24**
Block	2	3.44	0.62	11.37	5.25**	37.83
Error	48	4.23	7.81	6.34	0.68	224.52

Source of variation	DF	FSP	SSR MI	GWP (g)	FL (cm)	100-GW (g)
Mean	1	922593.38**	42.66"	117160.77**	97642.12**	525.20 ⁰ *
GCA	8	5513.07**	0.012**	134.92**	189.09**	0.26**
SCA	16	3293.65**	0.02**	107.20**	38.06**	0.06**
Block	2	73.29	0.01**	31.89	3.83	0.01
Error	48	131.854	0.002	19.768	4.924	0.017

** and *Significant at $p = 0.01$ and 0.05 , respectively. OF: Degree of freedom, DH: Days from sowing to initial heading, PH: Plant height, NPP: Number of panicles per plant, PL: Panicle length, NSP: Number of spikelets per panicle, FSP: Filled spikelets per panicle, SSR: Seed setting rate, GWP: Grain weight per plant, FL: Flag leaf length of main culm and 100-GW: 100-grain weight

Table 2: Estimates of GCA effects of the parents for 10 agronomic traits

Parents	DH	PH (cm)	NPP	PL (cm)	NSP	FSP	SSR (%)	GWP (g)	FL (cm)	100-GW (g)
Pei'ai64S	1.15*	2.57**	-0.23	0.78**	16.70**	18.04**	0.01**	-1.70	5.38**	-0.08**
NS30a	-1.99**	0.67	-0.99	-0.06	-7.31*	7.71**	-0.03	-1.80	-1.82**	-0.03
NS30f	-1.72**	-6.89**	0.12	0.63**	2.20	-46.12**	-0.04**	-1.63	-0.14	-0.18**
NS30h	0.28	1.33*	-1.41*	-0.38**	-15.56**	4.44	0.033**	0.71	-1.28*	0.26**
NS30g	2.28**	2.32**	2.51**	-0.98*	3.97	15.93**	0.03 ⁰ *	4.42**	-2.15**	0.07*
Minghui63	1.81**	1.73**	-3.28**	1.14**	-12.28**	9.34**	0.05**	4.08**	-0.95	0.15**
Rp5	-3.25**	1.65*	-0.19	-0.38*	-8.50*	3.48	-0.01	-4.62**	-0.50	0.03
Tt72	-3.19**	-11.80**	2.47**	-1.37**	-19.06**	-3.65	-0.004	1.70	-4.31**	-0.03
Sh633	0.75	2.62**	1.38*	-0.52**	18.78**	-4.26	-0.001	-1.45	-0.72	-0.02
Sh623	3.88**	5.81**	-0.39	1.13**	21.06**	-4.91	-0.04**	0.30	6.48**	-0.13**

** and *Significant at $p = 0.01$ and 0.05 , respectively. For abbreviations, see Table 1

line. While among the male lines, Minghui63 and Sh623 lines had the better GCA.

Estimation of specific combining ability ISCA): The SCA expresses the non-additive effect of genes. The results presented in Table 4. indicated that the characters depend not only on the GCA but also on the SCA. The SCA effects revealed that the cross combinations Pei'ai64S \times Rp5 for 100-

GW, NS30a \times Rp5 for NPP and NSP, NS30a \times Sh623 for FL, NS30f \times Minghui63 for FSP, NS30f \times Rp5 for DH, NS30f \times Sh633 for SSR and NS30h \times Sh633 for PL were the superior specific combinations as they showed high positive significant SCA effects. As for as the plant height is concerned, the negative estimates of SCA are desirable for reduced plant height and the good specific combination was NS30g \times Rp5 that had the highest negative significant of SCA followed by

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Table 3: Comparison of general combining ability effects for the parents Characters

Parents	DH	PH	NPP	PL	NSP	FSP	SSR	GWP	FL	100-GW	Total	Rank
Pei'ai64S	2	1	3	1	1	1	3	4	1	4	21	1
NS30a	5	4	4	3	4	3	4	5	4	3	39	5
NS30f	4	5	2	2	3	5	5	3	2	5	35	4
NS30h	3	3	5	4	5	4	1	2	3	1	31	3
NS30g	1	2	1	5	2	2	2	1	5	2	23	2
Minghui63	2	3	5	1	4	1	1	1	4	1	23	1
Rp5	5	4	3	3	3	2	4	5	2	2	33	4
Tt72	4	5	1	5	5	3	3	2	5	4	37	5
Sh633	3	2	2	4	2	4	2	4	3	3	29	3
Sh623	1	1	4	2	1	5	5	3	1	5	28	2

For abbreviations, see Table 1

Table 4: Estimates for SCA for 10 agronomic traits

Parents	DH	PH (cm)	NPP	PL (cm)	NSP	FSP	SSR (%)	GWP (g)	FL (cm)	100-GW (g)
Pei; ai64S*Minghui63	0.32	0.33	-0.77	0.15	4.74	-18.41**	-0.08**	-5.86**	-0.88	-0.20**
Pei'ai64S*rp5	2.39*	2.52	-4.30**	0.16	3.74	-7.53	-0.0024	3.98	-3.24**	0.24**
Pei'ai64S *tt72	-2.68**	2.25	-0.07	-1.11**	-17.37*	-1.75	0.14**	0.59	-0.71	0.20**
Pera64S`sh633	0.39	-1.84	6.13**	-0.11	14.91*	17.29*	-0.056**	4.03	4.68**	-0.16**
Pera64S*sh623	-0.41	-3.25*	-0.99	0.91*	-6.03	10.40*	0.0054	-2.74	0.16	0.08
NS30a*Minghui63	3.12**	-2.39	0.22	0.76*	-9.85	-17.26**	0.012	-4.49*	0.36	0.22**
NS30a*rp5	-3.15**	-1.64	6.69**	0.44	28.20**	13.77**	0.023	7.63**	-1.70	-0.16**
NS30a*tt72	0.45	2.48	-0.97	-0.04	-16.25*	-31.57**	-0.06**	-0.19	-0.02	-0.11
NS30a*sh633	-0.48	-0.04	-2.82*	-0.31	9.25	23.64**	-0.01	3.084	-5.34**	-0.0027
NS30a*sh623	0.05	1.59	-3.11**	-0.85*	-11.36	11.42*	0.03	-6.04**	6.70**	0.04
NS30f*Minghui63	-2.48**	2.28	2.99*	1.30**	2.73	51.53**	0.04*	2.89	0.24	-0.10
NS30f*rp5	3.25**	-0.90	-1.77	-1.01**	-10.08	34.99**	0.0002	-2.55	-2.14*	0.004
NS30f*tt72	0.52	-5.29**	1.91	-0.94*	5.80	33.89**	-0.08**	3.75	-0.15	-0.08
NS30f * sh633	-1.41	-0.38	-1.89	-0.15	-22.26**	-60.53**	0.16**	-5.95**	0.15	0.21**
NS30f*sh623	0.12	4.29**	-1.24	0.81*	23.80**	-59.88**	-0.12**	1.86	1.90	-0.03
NS30h*Minghui63	0.85	-0.86	0.30	-2.39*	8.22	-3.36	0.01	-2.77	-0.16	0.08
NS30h*rp5	-0.75	5.90**	-0.01	0.78*	-23.56**	-32.11*	-0.02	2.61	4.40**	-0.026
NS30h*tt72	1.19	2.45	0.28	1.23**	16.33*	-1.38	-0.01	-1.38	2.41*	-0.035
NS30h*sh633	0.59	-0.70	-1.19	1.60**	0.45	10.51*	-0.05**	0.63	0.09	-0.026
NS30h*sh623	-1.88*	-6.79**	0.63	-1.21**	-1.44	26.33**	0.08**	0.92	-6.74**	0.009
NS30g*Minghui63	-1.81	0.64	-2.74*	0.19	-5.86	-12.51*	0.02	10.23**	0.44	-0.004
NS30g * rp5	-1.75	-5.88**	-0.60	-0.37	1.70	-9.12	0.0002	-11.7**	2.70**	-0.061
NS30g *tt72	0.52	-1.89	-1.15	0.87*	11.48	0.81	0.02	-2.78	-1.52	0.02
NS30g*sh633	0.92	2.97*	-0.22	-1.03**	-2.36	9.09	-0.04*	-1.79	0.42	-0.016
NS30q *sh623	2.12*	4.12**	4.71**	0.35	-4.97	11.74*	0.008	6.00*	-2.03*	0.061

** and *Significant at p = 0.01 and 0.05, respectively. For abbreviations, see Table 1

NS30f×Tt72 combination. Only one cross NS30g×Minghui63 for GWP has high×high GCA showed high SCA effects and indicating the predominance of additive×additive type of gene effects for this character (Table 4).

The earliest hybrid (NS30a×Tt72) had parents with negative GCA effect, also had non-significant of SCA indicating the presence of additive×additive genes for this character. The crosses Pei'ai64S×Tt72 for PL, Pei'ai64S×Rp5 for FL and NS30g×Rp5 for GWP their parents had a positive and a negative GCA have combined to produce a hybrids with negative SCA effect for these characters, indicating the interaction effect between the different alleles. The hybrids Pei'ai64S×Minghui63 for FSP and Pei'ai64S×Sh623 for PH and NSP showed negative SCA value for these traits with high GCA value for parents, suggesting the presence of additive gene action for these traits.

Standard Heterosis: The magnitude of heterosis in F₁ hybrids is related not only to the performance of parents per se but also to the genetic diversity between two parents.

Positive as well as negative standard heterosis was observed for all characters, except for NPP and NSP, which showed positive standard heterosis for all the five hybrids (Table 5) while the SSR and 100-GW characters had a negative standard heterosis for all the five hybrids. Very high negative standard heterosis for FSP and PL was observed in NS30h/paternal hybrid while the hybrids NS30g/paternal and Pei'ai64S/paternal recorded highest positive standard heterosis for PL, FSP and GWP respectively. The highest grain weight of 30.57 g per plant in the hybrid NS30g/paternal was mainly due to increased NPP and FSP.

The results exhibited the F₁ heterosis of the combinations had late DH, strong PH superior, week SSR and 100-GW superior comparing with Shanyiu 10 (Table 5). Which suggested that we should pay more attention to GCA of above characters to improve sterile lines and restorer lines.

Combining ability and F₁ heterosis: Table 6 demonstrates the

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Table 5: Mean and standard heterosis % (in parentheses) of F₁ hybrid for 10 characters

Combination	DH	PH (cm)	NPP	PL (cm)	SP	FSP1	SSR (%)	GWP (g)	FL (cm)	100-OW (g)
Shanyiu 10 (CK)	81.17	97.47	12.00	24.13	138.60	120.00	0.87	33.66	36.10	2.97
Pei'ai 64S/paternal	84.20 (3.73)	103.56 (6.25)	18.933 (57.78)	25.44 (15.43)	178.64 (28.89)	128.95 (7.46)	0.72 (-17.24)	37.72 (12.06)	41.47 (14.88)	2.46 (-17.17)
NS30a/paternal	81.07 (-0.12)	101.66 (4.30)	18.12 (51.00)	24.60 (1.95)	154.64 (11.57)	118.62 (-1.15)	0.77 (-11.49)	37.82 (12.36)	33.93 (-6.01)	2.62 (-11.78)
NS30f/paternal	81.33 (0.20)	94.09 (-3.47)	19.29 (60.75)	25.29 (4.81)	164.14 (18.43)	107.65 (-10.29)	0.72 (-17.24)	37.90 (12.60)	35.95 (-0.42)	2.56 (-13.80)
NS30h/paternal	83.33 (2.66)	102.32 (4.98)	17.76 (48.00)	23.68 (-1.86)	146.39 (5.62)	115.35 (-3.88)	0.79 (-11.24)	40.23 (19.52)	34.80 (-3.60)	2.87 (-3.37)
NS30g/paternal	85.33 (5.13)	103.30 (5.98)	21.68 (80.67)	24.29 (0.66)	165.91 (19.70)	126.84 (5.70)	0.78 (-12.36)	43.95 (30.57)	34.27 (-5.07)	2.72 (-8.42)

Table 6: Correlation relation between GCA and Standard heterosis % of FI hybrids

Characters	DH	PH (cm)	NPP	PL (cm)	NSP	FSP	SSR (%)	GWP (g)	FL (cm)	100-GW (g)
Correlation value	0.999**	0.999**	0.998**	0.999**	0.882**	1.0**	0.988**	0.999**	0.999**	0.997**

** and *Significant at p = 0.01 and 0.05, respectively. For abbreviations, see Table 1

correlation relation between the standard heterosis and GCA. The results showed that there had high significant positive correlation relation between the standard heterosis of the hybrids and GCA effect of sterile lines for all the characters. Therefore, from GCA of sterile lines we can speculate compete superiors of sterile lines, but we can't confirm it is positive or negative superior. Also the results demonstrated that the higher GCA in parents, were stronger standard heterosis of hybrids. The sterile and restorer lines had lower GCA, for SSR and 100-GW, which also showed higher negative standard heterosis of the hybrids for these characters, suggesting it is difficult to use the sterile lines with lower GCA in hybrid production even though they have higher SCA. The GCA of GWP of sterile line was positive and negative, but standard heterosis of this character was positive for all the hybrids.

Discussion

The information on the magnitude of general and specific combining ability for different agronomic characters helps in understanding the gene action which is important for planning an effective hybrid rice breeding programme. The superiority of parents has to be assessed based on GCA of parents and its ability to produce specific combining hybrids. Additive and non-additive gene action in the parent, estimated through combining ability analysis, is useful in determining the possibility for commercial exploitation of heterosis (Ram *et al.*, 1998; Ganesan and Rangaswamy, 1998).

This study demonstrated that the majority of the crosses, showed significant SCA effects, which involved good and poor GCA, indicating additive x dominance type of gene interaction involved in the expression of characters. However, some crosses such as the combinations NS30a x Rp5 for NPP and NSP and NS30f x Sh633 for SSR involving low x low GCA showed high SCA effects, suggesting that epistatic gene action, might be due to genetic diversity in the form of heterozygous loci. It is reported that if the parents have lower GCA, but higher SCA cannot lead to strong heterosis of their hybrids.

By comparing SCA with GCA effects we found that the SCA effect of a combinations was not necessarily dependent on GCA effects of its parents. For example, GWP showed higher SCA effect in following combinations: NS30g x Minghui63,

NS30a x Rp5 and NS30g x Sh623 (Table 4). According to the GCA effects of their parents, the combining forms of these combinations were high x high, low x low and high x medium, indicating the genetic complexity of the character. This situation was also found in other characters. It implied that there was no necessary relationship between GCA and SCA effects. The result was accordant with another results reported by predecessor, (Gong *et al.*, 1993; Lu, 2000). This study showed that there had accordance between GCA effect and standard heterosis of the hybrids. The hybrids showed negative standard heterosis for SSR and 100-GW characters indicating little scope for improving these characters through exploitation of heterosis.

The study of combining ability is of great significance for hybrid breeding program. It may be easier to obtain strong heterosis by testing of SCA effects when GCA effects have been tested.

Acknowledgements

The first author would like to thank Prof. Sun C.X. of China National Rice Research Institute for his kind help and revision of this manuscript.

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